Published September 15, 2015

RESEARCH

Genetic Mapping of Race-Specific Stem Rust Resistance in the Synthetic Hexaploid W7984 × Opata M85 Mapping Population

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ABSTRACT

Stem rust (caused by *Puccinia graminis* f. sp. *tritici*) has historically caused severe yield losses of wheat (*Triticum aestivum* L.) worldwide and has been one of the most feared diseases of wheat and barley (*Hordeum vulgare* L.). Stem rust has been controlled successfully through the use of resistant varieties. However, stem rust lineage Ug99 and its derivatives are virulent to many widely deployed stem rust resistance genes including *Sr31*. Doubled haploid lines from the Synthetic W7984 × Opata M85 wheat reference population were screened for seedling resistance to *P. graminis* f. sp. *tritici* races TRTTF and QTHJC. The phenotypic data were adjusted to a 1 to 5 scale and genes for resistance to races TRTTF and QTHJC were localized using composite interval mapping (CIM). Major effect quantitative trait loci (QTLs) for resistance to stem rust races TRTTF and QTHJC were identified on chromosome arms 1AS, 2BS, 6AS, and 6AL. The gene for resistance to both races on 2BS could potentially be a new stem rust resistance gene. The QTLs for resistance on 1AS and 6AL might be other new genes or alleles while the QTL on 6AS is likely an *Sr8* allele. Future work will determine if the resistance loci on 1AS, 2BS, and 6AL are novel. As shown here, the well studied Synthetic × Opata reference population is a valuable source of potentially novel resistance genes for stem rust that can be leveraged in resistance breeding programs.

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Abbreviations: CIM, composite interval mapping; GBS, genotyping-by-sequencing; IT, infection type; LOD, logarithm of the odds; MQM, multiple quantitative trait loci mapping; QTL, quantitative trait loci.

Wheat stem rust, caused by *Puccinia graminis* Pers. f. sp. *tritici* Eriks. & E. Henn. (*Pgt*), has historically been a devastating disease of wheat and barley. Globally, stem rust has caused large losses of wheat yields in the 20th century in Europe and North America (Singh et al., 2006). Through eradication of the alternate host, barberry (*Berberis vulgaris* L.), and the deployment of varieties with genetic resistance, the yield and economic losses due to stem rust were reduced substantially (Singh et al., 2011). For decades, resistance to stem rust has relied on a handful of genes, including resistance gene *Sr31* (Singh et al., 2006).

In 1999, an isolate of *Pgt* virulent to *Sr31* was discovered in Uganda and named Ug99 (Pretorius et al., 2000). The original *Sr31*-virulent Ug99 isolate is designated as race TTKSK based on the North American nomenclature (Jin et al., 2008; Roelfs and Martens, 1987). Stem rust race TTKSK and variant races TTKST (virulent on *Sr24*) and TTTSK (virulent on *Sr36*) are virulent to most known resistance genes (Jin et al., 2008, 2009; Singh et al.,

Published in Crop Sci. 55:1–9 (2015).
doi: 10.2135/cropsci2014.11.0755

2006, 2008; Visser et al., 2010). Since its first discovery, the Ug99 race group has been detected in Kenya (2001), Ethiopia (2003), Sudan and Yemen (2006), Iran (2007), Tanzania (2009), and South Africa and Zimbabwe (2010) (Hale et al., 2012; Jin et al., 2009; Nazari et al., 2009; Pretorius et al., 2010, 2012). It is estimated that more than 66% of the global wheat growing area is environmentally conducive for the development of stem rust, and in much of this area, susceptible cultivars are grown (Pardey et al., 2013). Therefore, the discovery of new resistance genes with development of markers to facilitate marker-assisted breeding and strategic deployment in gene pyramids is critical.

The genetic diversity for resistance to stem rust in the hexaploid bread wheat gene pool is rather limited (Singh et al., 2011). A natural whole-genome hybridization of cultivated tetraploid wheat (*T. turgidum* L.) ($2n = 4x = 28$, AABB) and diploid wild species *Aegilops tauschii* Coss. ($2n = 2x = 14$, DD) about 8000 yr ago gave rise to the allohexaploid species known as bread wheat ($2n = 6x = 42$, AABBDD) (Dvorak et al., 1998; Kihara, 1944; McFadden and Sears, 1946; Talbert et al., 1998). Cultivated bread wheat went through multiple genetic bottlenecks during its evolution and domestication process and the diversity within modern wheat varieties has been narrowed further through modern crop improvement (Marcussen et al., 2014; Warburton et al., 2006).

Genetic diversity in the hexaploid germplasm pool can be increased through the production of synthetic hexaploid wheat by crossing tetraploid *T. turgidum* wheat with diploid *Ae. tauschii*. The development of synthetic hexaploids was first demonstrated by McFadden and Sears (1946). The technique has been iteratively improved and several research programs like International Maize and Wheat Improvement Center's (CIMMYT's) wide cross program have developed hundreds of primary synthetic bread wheat lines to capture genetic diversity from wheat progenitors (Reif et al., 2005; Zhang et al., 2005). Even though the primary synthetics generally have poor agronomic performance, they are known for harboring genes for tolerance to a range of biotic and abiotic stresses (Arraiano et al., 2001; Mujeeb-Kazi et al., 2004).

Triticum turgidum, has been a good source of new stem rust resistance genes including *Sr2*, *Sr9d*, *Sr9e*, *Sr9g*, *Sr11*, *Sr12*, *Sr13*, *Sr14*, and *Sr17* (Singh et al., 2011). Genes conferring resistance to race TTKSK are *Sr2*, *Sr13*, and *Sr14* (McIntosh, 1988; Simons et al., 2011; Singh et al., 2006, 2011). *Sr2* confers slow rusting adult plant resistance and is linked with the pseudo-black chaff (PBC) phenotype (Singh and Rajaram, 2002). It confers partial resistance to race TTKSK when homozygous and under low to moderate disease pressure (Mago et al., 2010; Singh et al., 2006). The recessive resistance gene *Sr2* is the primary component of the highly effective "*Sr2* complex" of several minor genes (Hare and McIntosh, 1979). Resistance gene *Sr13* confers resistance to race TTKSK (Jin et al., 2007). The sources of this gene are the Ethiopian land race ST464 and the emmer wheat cultivar Khapli (Klindworth et al., 2007; Knott, 1962). Like *Sr13, Sr14* was introduced from emmer wheat Khapli (Knott, 1962; McIntosh, 1980).

Six stem rust resistance genes or alleles from *Ae. tauschii* have been described including *Sr33, Sr45*, *Sr46, SrTA1662, SrTA1017* , and *SrTA10187* (Kerber and Dyck, 1979; Olson et al., 2013a, 2013b; Rouse et al., 2011). All are effective against TTKSK. Resistance genes *Sr33* and *Sr45* were incorporated into synthetic wheat by Kerber and Dyck (1979). Both, *Sr33* and *Sr45* originated from *Ae. tauschii* accessions found in Iran (Olson et al., 2013b). Resistance to several *Pgt* races has recently been identified in 98 *Ae. tauschii* accessions (Rouse et al., 2011). However, Rouse et al. (2011) were not able to postulate the presence of *Sr33, Sr45, Sr46,* or new genes in the accessions because of the complexity of the stem rust phenotypes. Recently, Olson et al. (2013a, 2013b) transferred *SrTA1662, SrTA1017* , and *SrTA10187* from *Ae. tauschii* by direct crossing between diploid *Ae. tauschii* and hexaploid *T. aestivum*.

Two synthetic wheat reference populations have recently been reconstructed by Sorrells et al. (2011). One is a doubled haploid population (named SynOpDH) and one consists of recombinant inbred lines (named SynOpRIL). Both populations were developed by crossing synthetic hexaploid line W7984 and elite bread wheat cultivar Opata M85 (Sorrells et al., 2011). The SynOpDH and RIL mapping populations were developed from the same parents as the original mapping population in the late 1980s. That population was also known as M6 × Opata, Synthetic × Opata, and ITMI mapping population. Here, we evaluated the recreated synthetic wheat doubled haploid mapping population (SynOpDH) for resistance to several stem rust races at the seedling stage to identify potentially new stem rust resistance genes.

MATERIALS AND METHODS

Mapping Population

The SynOpDH mapping population was developed by Sorrells et al. (2011). The pedigree of the population is synthetic W7984 (Altar 84/*Ae. tauschii* (219) CIGM86.940)/Opata M85. The population consists of 215 lines.

Genotypic Data

Genome-wide marker data on the SynOpDH mapping population was generated using a two-enzyme genotyping-by-sequencing (GBS) approach by Poland et al. (2012). The publicly available map and marker data were used to perform the QTL analysis. The previously constructed map consisted of 1485 single nucleotide polymorphisms (SNPs). Complete information about data filtering, SNP calling and map construction can be found in Poland et al. (2012). The female parental alleles from Synthetic W7984 were coded as "A", the male parental alleles from Opata M85 as "B". We verified the original assignment of the GBS markers to chromosomes and chromosome arms in

Poland et al. (2012) by aligning the tags to the recently published draft sequence of the wheat genome (The International Wheat Genome Sequencing Consortium, 2014). The linkage groups from GBS markers corresponding to chromosomes 1B, 1D, 2A, 5B, 6D and 7A were inverted to match the correct short and long chromosome arms, respectively. An updated map with corrected linkage group orientation and chromosome arm assignments is available in Supplemental Table S3.

Pgt Inoculation and Evaluation of Seedling Infection Types

The parents of SynOpDH, Synthetic W7984 and Opata M85, and a subset of the mapping population were screened with 14 *Pgt* races of diverse geographical origin at the USDA-ARS Cereal Disease Laboratory, Saint Paul, MN. Foreign *Pgt* races were evaluated in a biosafety level 3 containment facility at the University of Minnesota. Based on the observed segregation pattern, *Pgt* races TRTTF (from Yemen) and QTHJC (United States) were targeted for further mapping experiments.

Reactions to *Pgt* races TRTTF (isolate 06YEM34–1) and QTHJC (isolate 75ND717C) were evaluated in St. Paul, MN, following protocols described previously. The experimental design was a randomized complete block design (RCBD) with two replications of 10 seedlings per DH line for races TRTTF and QTHJC. Seedling infection types (ITs) to races TRTTF and QTHJC were evaluated in 127 and 100 doubled haploid lines, respectively. The stem rust susceptible wheat line LMPG-6 and the 20 lines of the North American *Pgt* differential set were included in the experiments as controls (Jin et al., 2008).

Urediniospores stored at −80°C were heat-shocked in a water bath at 45°C for 5 min and suspended in Soltrol 170 isoparaffin oil (Chevron Phillips Chemical Company LP, The Woodlands, TX). The suspension was sprayed onto 7- to 9-d-old seedlings and inoculated seedlings were placed in mist chambers overnight at 20±1°C at 100% humidity and then transferred to a greenhouse bench with a 16 h light/8 h dark cycle at 18±2°C. Infection types to both races were scored 14 d after inoculation using the scale of Stakman et al. (1962). Seedlings showing low and intermediate ITs up to 2+3- were considered resistant and seedlings showing high ITs of 3 to 4 were considered susceptible. The avirulence/virulence formula for TRTTF was 8a, 24, 31/5, 6, 7b, 9a, 9b, 9d, 9e, 9g, 10, 11, 17, 21, 30, 36, 38, McN, Tmp, $1RS^{Amigo}$ and for QTHJC 7b, 9a, 9e, 24, 30,31,36, 38, Tmp, $1RS^{Amigo}$/5, 6, 8a, 9b, 9d, 9g, 10, 11, 17, 21, McN (Jin et al., 2008; Olivera et al., 2012a).

The qualitative phenotypic data using the Stakman scale were converted to a 1 to 5 quantitative scale to enable analysis with QTL mapping algorithms that assume an ordered phenotypic distribution (Table 1). Low ITs with hypersensitive flecking including: ;, 0;, ;1, ;1+, ;2-, ;2, ;2+, 2-;, and ;12, were classified as 1. ITs of 2- to 2 were classified as 2. Lines displaying 2+ were classified as 3. Lines scoring ITs ranging from 2+3- and 32+ to 3 were scored as 4. High susceptible ITs of 3+ or 4 were scored as 5. The Stakman scale was converted for each replicate and then averaged across replicates. SynOpDH lines with missing data or inconsistent phenotypes (indicating mixed seed source) between replicates were removed before further analysis. The repeatability of the experiments was tested with the Pearson correlation coefficient after conversion to the 1 to 5 scale.

Table 1. Conversion of Stakman infection types to a 1 to 5 scale for mapping purposes.

Stakman infection types	Conversion
;, ;0;1, ;1+, ;2-, ;2, ;2+, 2-;, ;12	Class 1
2- to 2	Class 2
2+	Class 3
2+3- and 32+ to 3	Class 4
3+ to 4	Class 5

Table 2. Assessment of the resistance of the parents (Synthetic W7984 and Opata M85) of the mapping population with 14 different *Pgt* races from diverse origin.

Race	Isolate	Origin	Synthetic W7984	Opata M85
TTKSK	04KEN156/04	Kenya	3	33+
TTKST	06KEN 19-V-3	Kenya	33+	3+
TTTSK	07KEN 24-4	Kenya	3+	3+
TRTTF	06YEM34-1	Yemen	22-	22+
TTTTF	01MN84A-1-2	United States	3	4
TPMKC	74MN1409	United States	2+3-	2+3-
RKQQC	99KS76A-1	United States	;1	0;
RCRSC	77ND82A	United States	2 = ;1	;1
QTHJC	75ND717C	United States	;	2
QFCSC	06ND76C	United States	0;	0;
MCCFC	59KS19	United States	;1-	;1-
QCCSM	75WA1652-A	United States	0;	0;/;1+
QCCJB	01SD80-A	United States	0;	;1
SCCSC	09ID73–2	United States	;13-	0

Quantitative Trait Loci Analysis

Identification of stem rust resistance QTLs was performed in the R software environment (R Core Team, 2013) using the R-package R/qtl (Broman et al., 2003). The most significant markers were identified with stepwise regression separately for both *Pgt* races. Composite Interval Mapping (CIM) was implemented applying a Haley–Knott regression using forward selection of marker covariates and a window size of 10 cM for both stem rust races. Three marker covariates were used for CIM for races TRTTF and QTHJC. The map position and markers of QTLs identified by single interval mapping (SIM) and CIM were used in multiple quantitative trait loci mapping (MQM) (Arends et al., 2010) to confirm identified resistance loci and to refine their position. MQM was implemented in R/qtl to obtain estimated QTL effects. The genome-wide logarithm of the odds value (LOD) for declaring significant QTL for each race was determined by 1000 permutations. The parental alleles for Synthetic W7984 and Opata M85 were coded as –1 and 1, respectively, as described by Broman and Saunak (2009).

RESULTS

The parents of the SynOpDH population showed a wide range of ITs when tested with 14 *Pgt* races (Table 2). Both parents were observed to be susceptible to races TTKSK, TTKST, and TTTSK. However, both parents showed resistance to several *Pgt* races including TRTTF and QTHJC (Table 2). The observed IT of the synthetic

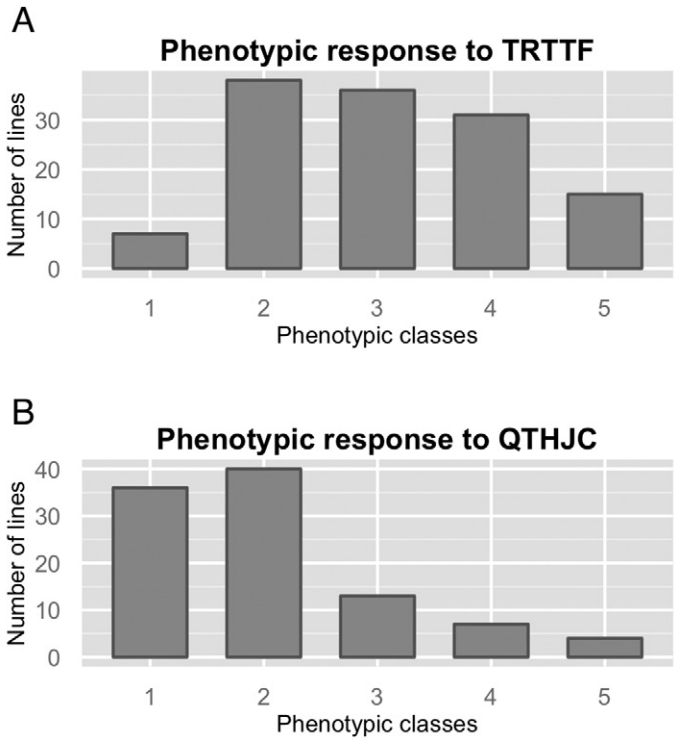

Figure 1. Phenotypic distribution of seedling infection types (ITs) to stem rust race TRTTF after conversion of the Stakman scale to a 1 to 5 scale as described earlier. Lines falling into categories 1 to 3 are considered resistant and lines in categories 4 and 5 are susceptible to stem rust race (a) TRTTF and (b) QTHJC.

Table 3. Number, segregation ratio, χ^2 and corresponding *P* values of SynOpDH lines showing resistance and susceptibility to *Pgt* races TRTTF and QTHJC.

Race	Resistant	Susceptible	Segregation ratio	χ^2	*P* value
TRTTF	108	19	7:1†	0.70	0.40
QTHJC	92	8	7:1	1.85	0.17
			15:1‡	0.52	0.47

† Segregation ratio for 3 gene model.

‡ Segregation ratio for 4 gene model.

parent to *Pgt* race TRTTF was 22-, and; to QTHJC. Elite parent Opata M85 showed ITs of 22+ and 2 to races TRTTF and QTHJC, respectively.

To test the repeatability of the experiments the Pearson correlation coefficient *r* was calculated for the DH lines. *r* values of 0.84 and 0.9 for QTHJC and TRTTF, respectively, indicated good repeatability of each experiment. The SynOpDH mapping population segregated for distinct resistance ITs to *Pgt* race TRTTF (Fig. 1a, Supplemental Table S1). Under the binary, resistant/susceptible IT designation, the SynOpDH population segregated 108:19 resistant/susceptible for race TRTTF (Table 3) not significantly different from a 7:1 ratio ($\chi^2 = 0.70$, $P = 0.40$), suggesting three resistance genes were segregating. Mapping revealed three QTLs for resistance to race TRTTF with a genome-wide LOD of 4.20 at a 5% error rate as determined by 1000 permutations. The three loci identified with CIM are located on 2BS, 6AS, and 6AL (Fig. 2). The QTL on 2BS is located proximal (most significant GBS marker is synopGBS355) at 53.8 cM. The other two QTLs are located on 6AS (GBS marker synopGBS1019 at 0.8cM) and 6AL (GBS marker synopGBS85 at 130.6cM) (Table 4).

The segregation pattern of resistance to stem rust race QTHJC showed a relatively larger proportion of lines was resistant to race QTHJC compared to race TRTTF (Fig. 1b; phenotypic data available in Supplemental Table S2). The SynOpDH population segregated 92:8 resistant/susceptible, which is not significantly different from either 7:1 or 15:1 ratios ($\chi^2 = 1.85$, $P = 0.17$; $\chi^2 = 0.52$, $P = 0.47$), suggesting three or four resistance genes were segregating. Quantitative trait locus mapping with CIM identified one QTL on 2BS (Fig. 2) with a genome-wide LOD of 3.70 at a 5% error rate. The marker with the highest LOD score on 2BS is located at 44.1cM (GBS marker synopGBS616). A second resistance QTL was located at 27.9cM on chromosome 1AS (most significant GBS marker synopGBS665) (Table 4).

The MQM is a useful tool to obtain estimates on phenotypic variance, QTL, and allele effects. The allelic state of the markers with the highest LOD score at each QTL was used to represent the allelic state of the QTL. For race TRTTF, a model with three genes and no interaction explained more than 60% of the phenotypic variance. The resistance genes on 2BS, 6AS, and 6AL explained 23, 13, and 26% of the estimated phenotypic variation, respectively (Table 5). The estimated allele effects show that the resistance to race TRTTF is conferred through alleles from both the synthetic and elite wheat parent (Fig. 3). The estimated QTL effect for the resistance gene on 2BS is 0.53 and 0.4 for the gene on 6AS with the resistant allele coming from the synthetic parent for both of these genes (Table 5 and Fig. 3). The resistant allele at the locus on 6AL was contributed by Opata and had an estimated effect of −0.57 (Table 5). Analysis of race TRTTF confirmed that resistant lines of phenotype classes 1 to 3 have either all three resistant alleles, or any combination of two out of the three identified resistance alleles.

For race QTHJC a model considering only one QTL on 2BS explains 26.7% of the estimated phenotypic variation. Including the QTL on 1AS the estimated phenotypic variation increases to 35.5%. Searching for further QTLs by means of MQM did not result in any LOD peaks over the set threshold. However, the LOD profile suggests the presence of a third resistance QTL on chromosome arm 1DL at 154.6 cM, barely below the threshold of 3.70 at an error rate of 5%. The estimated effect for the QTL on 2BS is 0.520 and 0.318 for the 1AS QTL. Based on the estimated allele effects both resistance QTLs are contributed by the synthetic parent (Table 5 and Fig. 3).

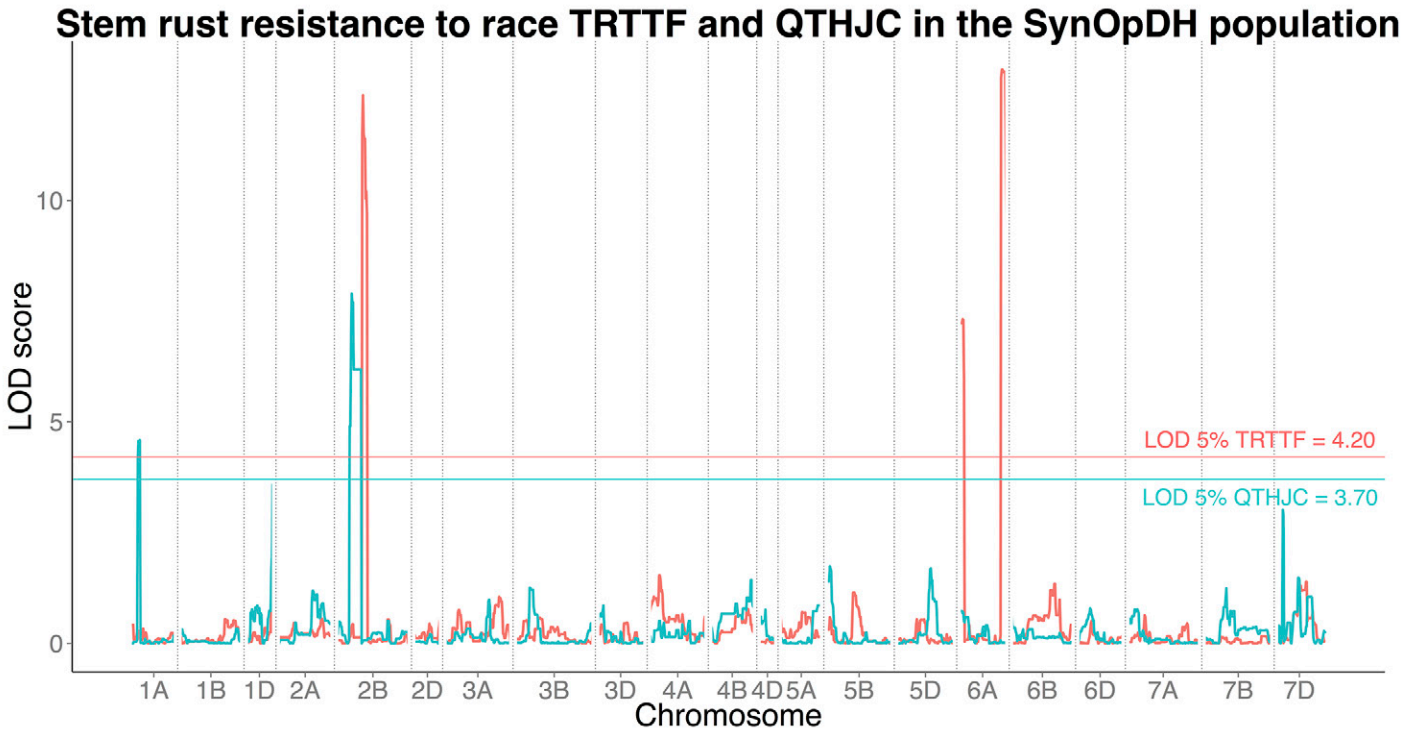

Figure 2. The logarithm of the odds (LOD) profile for stem rust resistance to both races TRTTF and QTHJC shows the identified resistance genes for race TRTTF in orange on chromosomes 2BS, 6AS, and 6AL (LOD 5% = 4.20), and for stem rust race QTHJC in turquoise on 2BS (LOD 5% = 3.70).

Table 4. Genotyping-by-sequencing (GBS) marker and quantitative trait loci (QTL) position for identified resistance QTL to races TRTTF and QTHJC.

Race	Chromosome	GBS Marker	Position
TRTTF	2BS	synopGBS355	53.8cM
	6AS	synopGBS1019	11.0cM
	6AL	synopGBS85	130.6cM
QTHJC	1AS	synopGBS665	27.9cM
	2BS	synopGBS616	51.8cM

DISCUSSION

This study identified three QTLs on chromosome arms 2BS, 6AS, and 6AL for resistance to *Pgt* race TRTTF and two QTLs on 1AS and 2BS for resistance to race QTHJC in the newly reconstructed synthetic hexaploid W7984 × Opata M85 wheat reference population. The estimated allele effects showed that resistance was conferred through alleles from both the synthetic hexaploid and the bread wheat parents. Based on the deduced chromosomal locations and the pedigree of the mapping population, only a few previously described resistance genes from durum wheat and bread wheat could be candidates for the QTLs identified here.

The resistance QTL on 2BS that was detected with race TRTTF was derived from the synthetic hexaploid parent and mapped to position 53.8 cM (Fig. 2 and 3). The resistance QTL for race QTHJC was initially mapped at 44.1 cM on 2BS. Applying MQM, the position of the gene was refined and newly positioned to 51.8 cM. Given the close proximity, it is possible that these effects for the two races are from the same resistance gene. Chromosome arm 2BS harbors at least seven numerically designated stem rust resistance genes, but many are on alien translocations (McIntosh et al., 2012). Resistance genes on 2BS from common wheat and durum include *Sr10, Sr19, Sr20*, and *Sr23*. Based on its position and presence in CIMMYT germplasm (McIntosh et al., 1995), *Sr10* is a potential candidate for the 2BS resistance QTL. However, both races TRTTF and QTHJC are virulent on *Sr10*, which, therefore, can be ruled out. Canadian spring wheat variety Marquis is the source of *Sr19* and *Sr20* (McIntosh et al., 1995) and has been used in crosses made at CIMMYT (Smale, 1996). Virulence was reported to be very common on *Sr19* and *Sr20* (McIntosh et al., 1995), but neither can be ruled out as candidates for the 2BS QTL. Stem rust resistance gene *Sr23* is completely associated with *Lr16* (McIntosh et al., 1995). However, *Lr16* was mapped at the distal end of chromosome 2BS (McCartney et al., 2005). Consequently, the mapped gene is likely not *Sr23* due to the different map position. Additional data are needed to determine the allelic relationship between the QTL mapped on 2BS and the numerically designated genes on 2BS.

The QTL for resistance to race TRTTF identified on 6AS was placed at 11cM distal following MQM. Based on its location, the QTL mapped to 6AS is probably conferred by *Sr8a* or *Sr8b* (McIntosh, 1972; McIntosh et al., 1995). *Sr8a* was first characterized from bread wheat and was widely used in lines developed in Europe and Mexico (McIntosh et al., 1995). The location of *Sr8* is at the distal

Table 5. Estimated phenotypic variance explained by each gene, estimated quantitative trait loci (QTL) and allele effects for detected resistance QTL to races TRTTF and QTHJC.

Race	Chromosome	Phenotypic variance	QTL effect	SE	Effect allele A	Effect allele B	Resistance from parent
TRTTF	2BS	23.1%	0.53	0.06	−0.53	0.53	Synthetic
	6AS	13.0%	0.40	0.06	−0.40	0.40	Synthetic
	6AL	26.4%	−0.57	0.06	0.57	−0.57	Opata M85
QTHJC	1AS	9.7%	0.32	0.08	−0.32	0.32	Synthetic
	2BS	24.4%	0.52	0.09	−0.52	0.52	Synthetic

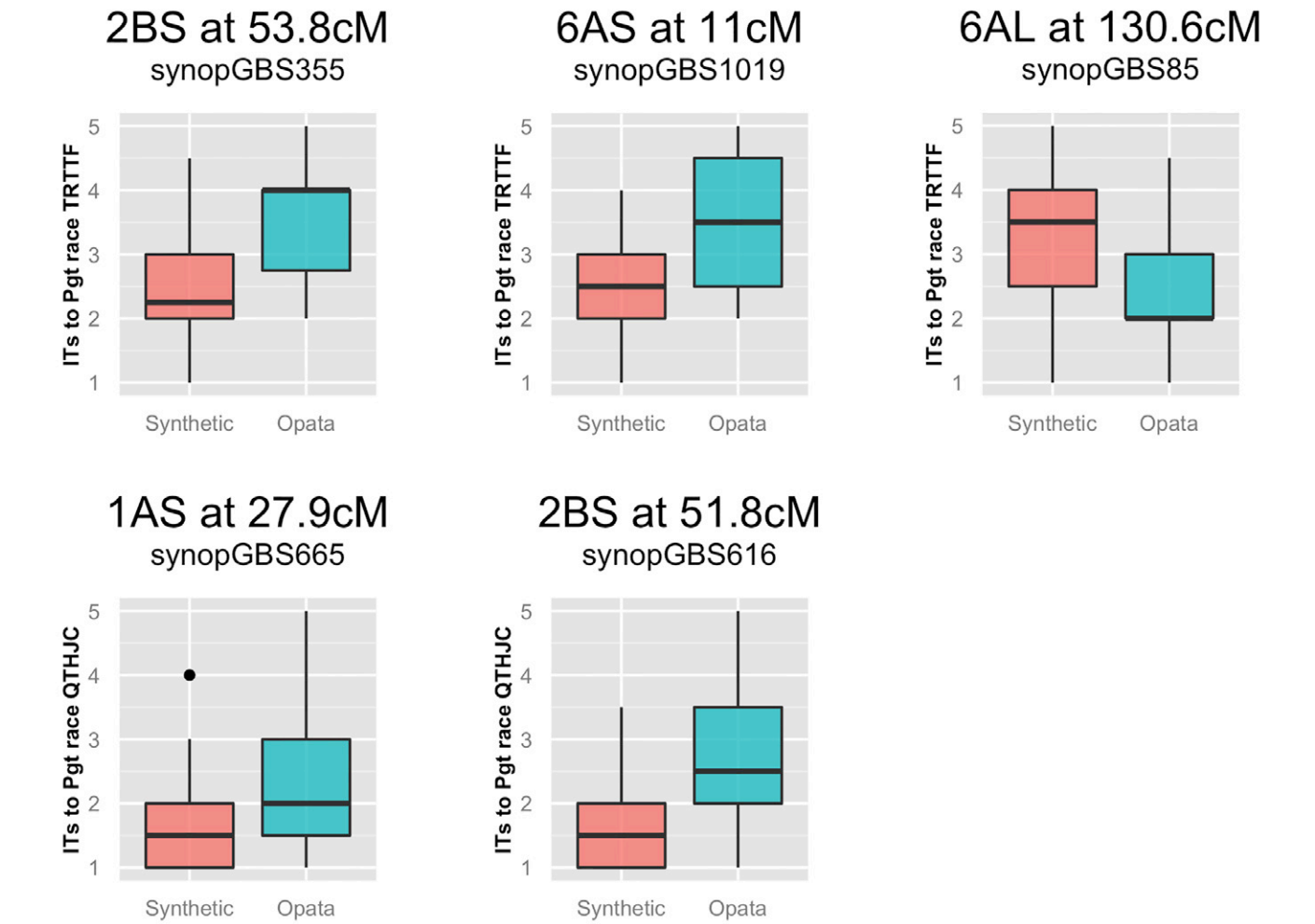

Figure 3. Estimated allele effects at each identified resistance quantitative trait loci (QTL) for both stem rust races TRTTF (above) and QTHJC (below). Allele A is the allele contributed by the synthetic parent, allele B by the elite parent Opata M85.

end of chromosome 6AS (GrainGenes2, 2013) and its location matches the resistance QTL. However, based on the allele effect of −0.402 for allele A the resistance gene was contributed by the synthetic parent. *Sr8b* is known to be present in durum wheat (Bhavani et al., 2008). Race TRTTF is avirulent to *Sr8a* whereas race QTHJC is virulent. The response of both races to *Sr8b* is unknown. Additional data are needed to determine the relationship between the QTL on 6AS and the two *Sr8* alleles.

The gene located on 6AL maps to the region of *Sr13,* which is known to confer resistance against TTKSK and its variants TTKST and TTTSK (Klindworth et al., 2007). However, both parents showed susceptible ITs to all three races (Table 2) indicating that this identified resistance locus is not *Sr13.* Furthermore, TRTTF is virulent on *Sr13* (Olivera et al., 2012b). Therefore, the gene mapped on 6AL is likely a new gene or a novel allele of *Sr13.*

For race QTHJC, segregation ratios of 7:1 and 15:1 suggest three or four resistance genes. However, only two resistance QTLs on chromosomes 1AS and 2BS were identified with confidence. Based on the LOD profile, two additional QTL may be on chromosome arms 1DL and 7DS. Opata is known to carry the pleiotropic gene designated *Lr34/Yr18/Sr57*, which is an adult plant resistance gene on 7DS. It is possible that *Sr57* has a detectable effect at the seedling stage, especially in combination with

other genes. One resistance gene has been reported on 1AS that originated from the 1AL.1RS wheat–rye translocation (Lein, 1975; McIntosh et al., 1998). However, this mapping population does not harbor this translocation, and, therefore, the resistance QTL identified here might be conferred by a new resistance gene. It is possible that the allele effect of each susceptible allele was not properly estimated due to some other gene(s) conferring resistance. This might lead to confounding estimations of the number of resistance genes. Further experiments will be needed to determine the mechanism of resistance to race QTHJC before proceeding with fine mapping and marker development for marker-assisted selection.

Through screening the SynOpDH reference mapping population for stem rust resistance, we have identified multiple resistance loci to the highly virulent *Pgt* race TRTTF and United States race QTHJC. Based on the virulence patterns and locations of known resistance genes, we conclude that the QTL on 6AL and 1AS could be new genes or new alleles of known genes. Additional data are needed to determine the relationship between the QTL on 2BS and 6AS and known genes on these chromosome arms. With the continued identification and marker tagging of effective stem rust resistance genes, the tools available to breeders for developing resistant breeding material and new varieties will further improve.

Supplemental Information Available

Supplemental information is available with the online version of this manuscript.

Acknowledgments

The Graduate Research Assistantship of S. Dunckel is supported through the Monsanto Beachell-Borlaug International Scholars Program. This work was done under the auspices of the Wheat Genetics Resource Center (WGRC) Industry/University Collaborative Research Center (I/UCRC) supported by NSF grant contract (IIP-1338897) and industry partners. This work was funded by the U.S. Agency for International Development (USAID Cooperative Agreement no. AID-OAA-A-13-0005), the United States Department of Agriculture-Agricultural Research Service (Appropriations no. 5430-21000-006-00D and no. 3640-21220-021-00) and The Bill & Melinda Gates Foundation through the Durable Rust Resistance in Wheat project to Cornell University. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture. USDA is an equal opportunity provider and employer. This work represents contribution number 15-415-J from the Kansas Agriculture Experiment Station (KAES). Conflict of interest: The authors declare that they have no conflict of interest.

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